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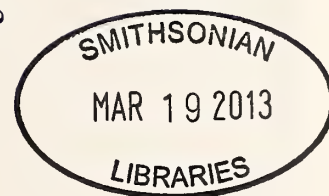
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WHAT DOES IT MEAN TO BE HUMAN? A BEHAVIORAL PERSPECTIVE

by Alison S. Brooks

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"...it would be impossible to fix on any point when the term "man" ought to be used....." (Darwin 1871: 230)

A new permanent exhibit at the Smithsonian's National Museum of Natural History asks the question "What does it mean to be human?" Before there were any fossils to inform us about the roads taken and not taken on our evolutionary journey, 18th and 19th century scholars wrestled with the anatomical similarities between humans and apes, especially, as Darwin noted, the African apes. Many of the human distinctions these early scholars cited were behavioral, including language, tool-making and technology-dependence, culture, use of fire, a sense of shame, burial of the dead, and a sense of the sacred. Even today, our anatomy alone may not suffice to define our genus *Homo*. Indeed in 1964 one of the oldest members of our genus, *Homo habilis*, was defined as *Homo* to a large extent on the basis of the tools found in association with its bones; the evolutionary or generic status of the bones themselves remains controversial. As in the museum's new exhibit, new approaches to understanding our past and defining our species emphasize the

role of changing human behavior and its relationship to and possible role in changing our anatomy.

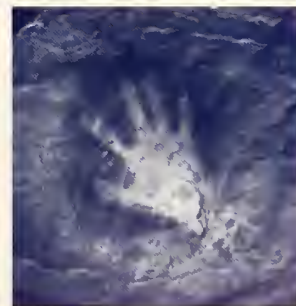
This paper offers a brief summary of key discoveries in the fossil record followed by a discussion of behavioral characteristics defining modern humans and their emergence through time. This is followed by a description of the evidence documenting the development of archaic, Neanderthal, and modern humans, tracing the evolution of key behaviors from 600 kya to 40 kya (thousands of years ago). Finally, the evidence for the role of Africa in the gradual evolution of distinctly modern human behaviors is argued as the paper concludes.

The Fossil Record of Human Evolution

Charles Darwin in his 1871 book, *The Descent of Man*, located the likely origination of humans in Africa due to the geographic distribution and comparable anatomy of the chimpanzee and gorilla. Other early scholars, however, thought that our two most distinctive anatomical features, our large brains and our two-legged gait, had evolved together and that these changes had happened in Europe. In Darwin's time, only a few fossils of Nean-

SPECIAL ISSUE ON HUMAN ORIGINS

What Does it Mean to be Human?



Smithsonian
National Museum of Natural History

derthals, our closest extinct relatives, had been recovered from European sites. The 1891 finding in Java of *Pithecanthropus erectus* (now *Homo erectus*), an upright biped with a cranial capacity of only 900cc., argued that both of these ideas were false; bipedalism came first and not in Europe. Only much later in 1924 were the first African fossils of human ancestors recovered at Singa (Sudan) and Taung (South Africa). The ca. 2-2.5 million-year-old Taung specimen of a small child with a chimpanzee-sized brain became the type fossil of *Australopithecus* (Dart 1925), a genus that is probably ancestral to our own (*Homo*). Like the *Pithecanthropus* discovery, the Taung child's human-like teeth, small brain but upright posture, as indicated by the position of the skull on top of the spine, suggested that brain development lagged behind new ways of getting around.

Most scholars in the 1920s, and some much more recently, continued to argue that major changes in the human evolutionary past occurred in Eurasia. But since the 1920s, Pliocene and Pleistocene age (5.3 – 0.01 million years ago or mya) fossil specimens belonging in the hominin lineage—representing more than 6,000 individuals—have been recovered at an accelerating pace from Europe, Asia, Africa, and Australia. Africa has yielded the oldest members of the human lineage (“hominins”), the oldest stone tools, the oldest members of our genus *Homo*, and the oldest members of our species *Homo sapiens*. Multiple genetic studies of modern human mitochondrial Y-chromosome and nuclear DNA conclude that the greatest variability, the most ancestral lineages, and the likely region of origin are all African, proving that Darwin was right in assigning us an African origin.

The emergence of a richer fossil record raises anew the question, what do we mean by human? Are the earliest hominin fossils from 7-3 mya whose skeletons reflect some level of bipedal locomotion human? (See accompanying article on the development of bipedalism.) Does the genus *Homo* begin with the appearance of stone tools 2.6 mya, or with the first reduction in molar size around 2.3 mya, or with the first signs of brain enlargement in Ethiopian and Kenyan fossils from 1.9 mya? Should we only bestow the word “human” (or the generic/evolutionary status of *Homo*) on fossils with the human-like suite of characteristics reflected in the relatively complete skeleton of the 1.5 mya “Turkana Boy.” Found in northern Kenya, this fossil had a brain almost 2/3 the size of ours, smaller

teeth than in previous hominins, and modern body size and limb proportions reflecting fully-committed bipedal walking and running. Should we limit the definition of “fully human” only to members of the species *Homo sapiens*, defined morphologically by large brains in relation to body size, small teeth, gracile skeletons, chins, minimal brow ridges, vertical foreheads, and faces tucked under braincases in such a way as to facilitate speech? Or perhaps only to those members of our species who demonstrated advanced abilities for symbolic behavior, innovation, and social complexity?

A Behavioral Perspective

Like the expanding fossil record, studies of great apes in the wild have documented many human-like behaviors, blurring humans' behavioral distinctiveness. All the great apes make and use simple tools, and their tool use and other behaviors vary among populations, suggesting that groups invent and hand down different behaviors from one generation to the next, a rudimentary form of ‘culture.’ While spoken language is still a major defining feature of humans, many humans use other forms of communication, and some apes have proven capable of learning from humans or even from each other to communicate using elements of sign language. Psychologists focus on the expression, in humans, of such characters as “empathy” and “problem-solving abilities.” However, in almost every case, at least one of the great apes (or some other animal) has shown this feature in some form. An absolute distinction between humans and non-human animals has thus far proved elusive.

What can the fossil and archaeological records tell us about the evolution of human behavior? Even before there are any tools or archaeological sites, the fossils themselves reflect behavior in the shape of bones, the position and strength of muscle markings, the form of the teeth, the patterning of reinforcing structure inside the bone and its chemical composition, as well as in signs of trauma over a lifetime. The long arms, curved fingers and toes, and upwardly-oriented shoulder joint of *Australopithecus* reflect a life still lived partially in the trees. Small canines suggest a new, less confrontational approach to male-male relationships and social organization, while chemical studies of the teeth suggest that later ones may have begun to exploit the same foods that make up large parts of the human diet – meat and tubers. The reconstructed environments of the

sites themselves also tell a story—of early use by hominins of a wide range of environments both in and out of the forest.

Between 2.6 and 2.3 million years ago in Ethiopia and Kenya, along with *Australopithecus* and some fossils with slightly smaller teeth and shorter faces attributed on that basis to *Homo*, we begin to find material remains in the form of flaked stone tools and bones that were cut and broken open to access meat and marrow. Such archaeological sites are formed through human activities, although it has been shown that chimpanzees also leave archaeological traces of their behavior.

The fossil and archaeological records are limited in what they can say about the origins of humans, as they require definitions of humanness that are amenable to recovery in the material record. For example, one cannot recover fossil languages, at least not until the development of writing. But one can recover traces of symbolic behavior, or morphological traces of changes in brain or vocal tract morphology that suggest an ability for language. Ideologies or the capacity for abstract thought are not preserved, but one can recover traces of practices that seem to conform to ideas about spirituality—burial of the dead and cave art. Problem solving and creative innovation cannot be directly observed in the past, but one can document increases in technological sophistication and rates of innovation. Social networks and societies in which humans live are abstractions that must be inferred from physical evidence even in living populations. But through geochemical analysis of where raw materials came from, one can trace the movement of materials like stone and beads over very long distances and thereby infer human networks' size and distance.

In addition, from patterns of variability in the material record, it is possible to infer whether or not people distinguished themselves from their neighbors through their material culture, and what the size of the distinctive groupings might have been. Signs of empathy may also be evident in the survival of individuals with crippling injuries or major deficits, who could not have survived long on their own.

Defining Human Behavior

From the perspective of modern humans, behavioral definitions of humanness include what can be considered “living in our heads,” enabling us to transform the natural world.



Multipurpose tools, such as hand axes, used to chop wood, butcher animals, and make other tools, dominated early human technology for more than a million years. Left to right: Africa (1.6 million years old), Asia (1.1 million years old), and Europe (250,000 years old). Photo courtesy Human Origins Program.

Humans think up cultural solutions to scarcity, risk, and the quest for food, shelter and mates, resulting in an astounding diversity of cultural forms and the transformation of vast areas of the earth's surface. Since humans' teeth and their two-legged gait are utterly inadequate for defense against natural predators, humans are totally dependent on invented technologies. Rather than living in a physical herd or a pack, humans live in what have been called “imagined communities,” populated by individuals never physically encountered—distant relatives, compatriots, ancestors, and spiritual beings. Humans use symbols extensively to represent themselves, their social groups, and their thoughts. Humans have the ability to imagine the feelings and lives of others as both separate from and similar to their own—in a way that leads to extraordinary capacities for altruism and sympathy, even for individuals they may never meet.

One way to describe the capabilities of modern humans is to separate out at least six different faculties:

Abstract thinking, the ability to act with reference to concepts not limited in time and space. A chimpanzee can be taught to use symbols correctly to solicit a reward, but not to go to the grocery store with a shopping list and remember that she forgot to write down the bananas.

Planning depth: the ability to strategize in a group context. Social carnivores share this ability in the immediate future, but lack our ability to plan for next year, or for contingencies that may never happen.

Problem-solving through behavioral, economic, and technological innovation: Many animals are good problem solvers, but modern humans solve problems that have not yet arisen and devise entirely new ways of living in the process.

Imagined communities: Our present communities, from family to nation, may include people we have never met, spirits, animals, and people who have died and the not-yet-born. These communities exist in our heads and never meet face-to-face as a group.

Symbolic thinking: Especially with regard to information storage, this involves the ability to reference both physical objects/beings and ideas with arbitrary symbols, and to act on the symbol even if the person who planted it is no longer present. It is both the arbitrariness of such symbols and their freedom from time and space constraints that distinguish our symbolic behavior from that of animals and constitute the foundations of human language.

Theory of mind: The ability to recognize oneself as a separate intelligence but at the same time to read the emotions and thoughts of others (empathy). Apes and even domestic carnivores possess this to a degree, but only modern humans can respond to humanity in individuals they will never meet.

The Early Record: 2.6 - 0.6 mya

If all these are key human abilities, when did they first appear? It is difficult to say, not only because the record is sparse and patchy, but because the capability may or may not be expressed for hundreds or thousands of years after it appears and may depend on the development of other factors or historical events. The capability for inventing computers may have existed in the late Pleistocene, but could not be expressed without the appropriate cultural and technological milieu. The limited evidence for these characteristics' early expression suggests, however, that the total package was not assembled over a short period.

Problem-solving and technological innovation. The first stone tools date to 2.6 mya from Ethiopia, slightly later in Kenya. There is little evidence for abstract thinking in these artifacts as they consist of simple flakes directly related to the form of the raw material, although the ability to choose appropriate raw materials and to derive multiple flakes from

a single block is far beyond what even the smartest apes can be taught to do. The rate of change or innovation is initially very slow; new forms such as bifacially worked symmetrical handaxes appear only after the first 900,000 years; and tools remain static for more than 1 mya after that. Nevertheless, such tools made it possible for early humans to shift from the largely frugivorous diet of the great apes to a diet with substantial carnivory and exploitation of new foods such as underground tubers. By 1.9-1.6 mya, our early ancestors also could expand into the Near East, Indonesia, and China, far beyond their original range and adapt to the new environments and faunas there. Technology also seems to have made possible a shift in food preparation from teeth to tools, so that teeth became smaller while body size increased. Early human diets were probably omnivorous, with meat obtained largely by scavenging. Fire was controlled by 0.8 mya or earlier, facilitating a new diet, the use of caves, hunting, new technologies, and social time at night.

There is no evidence from this time for *imagined communities* or *symbolic thinking*. Stone and other materials appear to have largely derived from within about 15 miles (25 km) of the site. Technologies are very similar from India to England and from France to South Africa.

Empathy, which appears very early in modern children before competent speech, may already be reflected in a very early human skull from Dmanisi in the Caucasus at 1.9 mya. The individual had lost almost all his teeth a considerable time before death, a condition rarely found in wild primates. Survival of this toothless individual required either a new, very soft diet or the assistance of others.

The early appearance of these features does not mean they were as fully expressed as in modern humans or even that the full capacity existed as in ourselves. But it does indicate that the human capacities do not arise suddenly in full-blown form but rather develop over time from less human antecedents.

Late Archaic Humans and Neanderthals: 600 kya to 40 kya

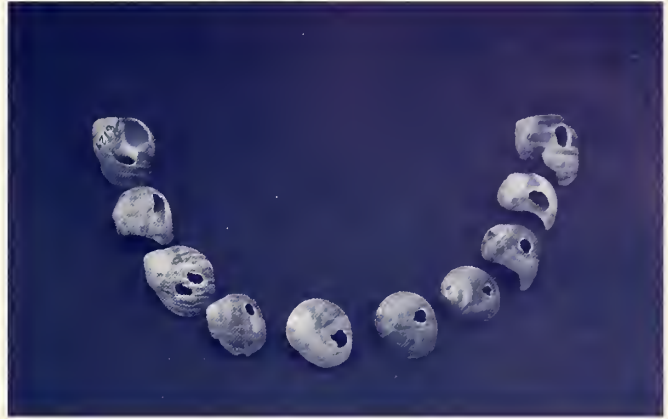
Beginning before 600 kya (thousands of years ago), most fossils in Africa, Europe, and the Near East present essentially modern brain sizes, although their teeth and faces are still large. In Africa, this shift may coincide with a new stone technology (Levallois), requiring a greater degree of ab-

tract thought to imagine the flakes whose shapes were predetermined by the shaping of the cores. Evidence of an increase in technological innovation, larger social networks or symbolic behavior, however, is minimal until ca. 400 kya, although new evidence of an occupation of southern England ca. 700 kya years ago suggests the ability to meet the challenges of a much more temperate environment. Ocher's increased use in Africa by 240 kya or earlier may suggest body painting or alternatively a more utilitarian function. Wooden spears or javelins from Germany and numerous remains of large animals imply a more complex hunting technology, which may have facilitated the occupation of much higher temperate latitudes.

Neanderthals, who occupied Eurasia as far east as Uzbekistan between ca. 250 and ca. 35 kya (or even later in a few 'refuge' areas) were significantly more like modern humans in their behavior than their predecessors. They buried their dead, but without clear evidence of grave goods or associated symbols, used black and red mineral pigments found as powder, lumps and "crayons," made stone-tipped spears, and were competent hunters of large game. Their fossil remains bear traces of both interpersonal aggression, in the form of a knife wound, and empathy, as elderly and handicapped individuals survived for much longer periods than previously. Although Neanderthals occupied Europe for at least 200 kya, their technology shows very little innovation or regional differentiation until the last 15 to 20,000 years of this time. The Neanderthal brain was similar in size to ours when adjusted for their larger body mass, but the relationship of the tongue and soft palate to the laryngeal space suggest that they may still not have been capable of all the complex speech sounds made by modern humans. Personal ornaments are only found at the most recent Neanderthal sites, after 50 kya, dating to a time when anatomically modern humans were already on the periphery of Europe. Does this mean the Neanderthals possessed a capacity for innovation and symbolic behavior, or only a facility for imitation?

Modern Humans, *Homo sapiens*: An African Origin

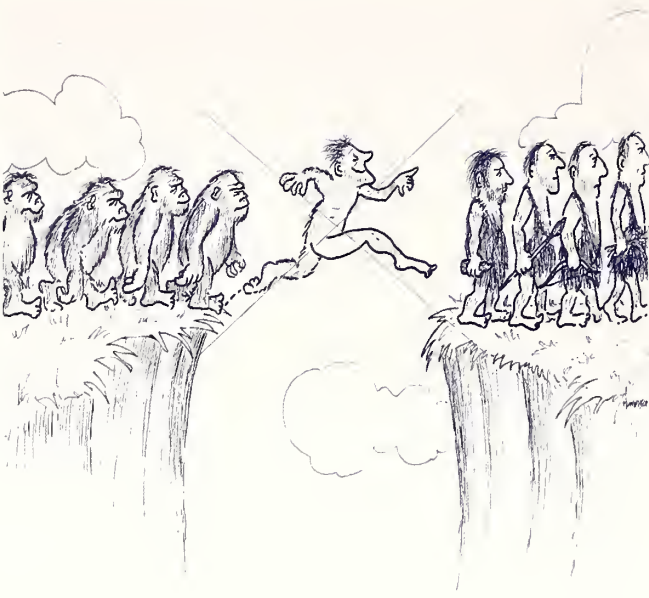
Into the 1970s it was thought that modern humans evolved in Europe. But with the advent of new fossils and better dating techniques, it has become clear that the oldest anatomically '*Homo sapiens*' fossils were African. The oldest fossil



These 30,000-year-old shells from Cro-Magnon, France, represent some of the earliest evidence of humans wearing jewelry. Some shells have traces of ocher, a clue they were colored with pigment. Photo courtesy Human Origins Program.

attributed to *Homo sapiens* in Africa is more than five times as old as the oldest *Homo sapiens* in Europe. At the same time, genetic studies demonstrate that all living humans share a 'recent' African common ancestor who lived between 100 and 200 kya. One group of African genetic lineages shares a common ancestor with all non-Africans that is considerably younger, perhaps 40-80,000 years ago. Although at first these results were disputed, repeated genetic analyses have confirmed our African origin. DNA sequences have been recovered from Neanderthals who lived as far apart as Spain and Siberia. The resulting sequences share similarities with one another but indicate at least three regional populations and contain many sequences not shared with living humans, suggesting at least 400 kya of separate evolution.

The rapid appearance of modern-looking people in Europe was not a punctuated "human revolution" or "great leap forward." It was an invasion of people with long tropical limb proportions. Asia has a more complicated but equally punctuated history, also suggesting invasion and ultimate dominance by outsiders. Indeed the first "out-of-Africa" migrations of *Homo sapiens* were to the Near East, with modern humans appearing first at Skhul and Qafzeh in Israel between ca. 110 and 90 kya, an initial wave that does not appear to have spread beyond this region until 50-60 kya. Modern humans then disappear from the Levant, as Levantine fossils from 90-50 kya are all Neanderthals. Modern humans expand again at or before ca. 50 kya.



"Rapid appearance of modern-looking people in Europe was not a great leap forward."

Modern Humans: Revolution or Gradual Evolution?

The earliest *Homo sapiens* in Europe and Asia, ca. 40 kya and later, were almost certainly capable of the same range of behaviors as we are, as indicated by their cave paintings, sculptures, musical instruments, beads and other jewelry, trade networks, technological innovations, regional diversity, economic flexibility, and ability to colonize the entire globe. There is considerable debate about earlier humans in Africa who were physically similar to us in many ways. Some scholars argue that they were physically modern but behaviorally primitive. To these scholars, modern behavior came about suddenly, a "Human Revolution" tied to a rapidly spreading genetic mutation for language.

In a 2000 paper, Sally McBrearty and I argued otherwise, that the capabilities for these behaviors began to be expressed and therefore existed even before modern physical appearance, with a gradual assembly of the kinds of behaviors we see later. This assembly was not unilineal but geographically and temporally spotty, with many reversals.

Archaeologists look especially for technological innovation and complexity as proxies for problem solving; for long-distance exchange and economic intensification as proxies for both planning depth and imagined communi-

ties; for regional styles that change over time as proxies for symbolic thinking and/or imagined communities; and for beads, images, and notational pieces along with burial of the dead as proxies for abstract and symbolic thinking and theory of mind. For all of these material expressions of behavioral capabilities, there are modern, even living groups without them. While demonstrably capable of producing such items, these groups clearly lack the impetus or the history to do so, so absence may not be a good marker of non-modernity. But absence of all of these over long archaeological stretches of time cannot be characterized as "modern behavior."

Since 2000, the rapidly accumulating record of human behavioral evolution in Africa has confirmed, rather than contradicted, our basic model of an earlier and more gradual accumulation of complex behaviors expressed in material culture. Beads, decorated ocher and ostrich egg-shell, innovative technologies involving hafted projectiles, and even the possibility of complex projectile weapons systems, have all been argued for Middle Stone Age (MSA) peoples predating 60 kya. Furthermore, new dating and study of previously excavated materials have shown that burials of *H. sapiens* with grave goods are found both in South Africa and in the Near East, dating to 66-90 kya and 90-100 kya, respectively. These burials suggest that symbolic behavior characterized at least some of the early members of our species long before the main "Out of Africa" event suggested by genetic dating.

But after more than a million years with little change in technology, the African record suggests that well before the first appearance of *Homo sapiens*, even before 285 kya, behavior had begun to change. New technologies produced standardized stone flakes and long thin blades, ocher processing increased, and many sites have small quantities—up to 5%—of stone material derived from sources a considerable distance away, as much as 125 miles (200 or more km)—the first sign of an expanded social network. The behavioral changes reflected in these finds are not sudden or directional. The evidence for them is interspersed with sites containing the old symmetrical large cutting tools, or simple flake technologies, or lacking evidence for ocher or exotic stone. But the general trend is towards more complex behaviors with time. Importantly, by ca. 267 kya, several sites in South and East Africa include carefully made stone points, designed for hafting onto spear shafts.

New Technologies

More dramatic changes in behavior occur after the appearance of *Homo sapiens*. From South Africa to Egypt and from the western Sahara to Ethiopia, evidence for complex technologies and new tools increases especially after 100 kya. In Ethiopia, the first *Homo sapiens* at about 195 kya are associated with advanced flake technologies but the older symmetrical large cutting tools continue at some sites in the Horn of Africa. Before 90 kya, stone points are large or thick, and were likely hafted onto thrusting spears used in close encounters with prey. But after 90 kya, the points become tiny and light. Possibly these very small later points, which could not have delivered a lethal blow to a large animal, were hafted on the ends of spear thrower darts or arrows, and even associated with the use of poison.

As early as 130 kya, another set of technological innovations appears to have focused on fishing. In the eastern Democratic Republic of Congo (Zaire) our team discovered a series of what appeared to be Middle Stone Age localities along the river. Excavations at three sites revealed mammalian fauna and lithic artifacts but also a series of barbed bone points associated with thousands of fish bones. The dates for these sites have varied, but luminescence dating suggests an age of 80-90 kya, and there is no evidence for an age less than 60 kya. Again, this is a complex technology that appears to have been outside Neanderthal competency.

Small projectile armatures in a complex weapons system could have given the edge to later modern humans, allowing populations to expand both within and outside Africa at the expense of the Neanderthals and other archaic populations. Neanderthals had many injuries from personal encounters with large dangerous animals, but later moderns had very few. Neanderthals also had many more signs of dietary stress in their bones and teeth than the early moderns who succeeded them.

Long-Distance Exchange

At several sites in East and Central Africa, some stone tools made by early modern humans use stone that does not come from the local area. Throughout East Africa there is a preference in many sites for obsidian, a fine black volcanic glass with very specific chemical characteristics. In many areas, such as the Aduma area in the Middle Awash region

of Ethiopia, obsidian sources do not occur in the immediate vicinity of the sites, and the obsidians themselves are varied and appear to derive from multiple sources. When the chemistry of the obsidian can be matched to specific sources, as at Mumba in Tanzania, it suggests that obsidian was being moved more than 125 miles (200 km) in some cases. This suggests the existence of trading networks, or “imagined communities.” Distant trading networks would benefit from the use of symbols to identify members of such a community, so it is not surprising that ochre and other minerals were also processed for pigment at some sites such as Twin Rivers in Zambia, as early as 240 kya. Other indicators of imagined communities are the regional “styles” of projectile points that possibly identify social entities in space.

Symbolic Behavior

So far, we have demonstrated the presence of technological innovation, economic intensification, long distance exchange, and regional styles in the behavioral repertoire of early modern humans. But is there hard evidence for symbolic behavior? In 2002, an extraordinary piece of engraved ochre was described from Blombos cave in South Africa. It and a second similar piece clearly suggest that ochre had more than a utilitarian function. Many other pieces of ochre, bone, and eggshell with engraved geometric or linear designs are known both from this site and from other southern African sites, including fragments of decorated ostrich eggshell containers from ca. 65 kya at the Atlantic coastal site of Diepkloof.

Beads and other body ornaments are unequivocal evidence for symbolic behavior and for fully human status, as they have little utilitarian function. In traditional hunting societies, beads provide the basis of exchange networks that served to tie distant people together in a mutual support network, particularly useful when times are bad. Individuals deliberately build these networks up as they grow into middle age and acquire major responsibilities for raising and marrying off children or for supporting elderly parents. As they age and their needs decrease, individuals begin to reduce the size of these networks.

Beads and personal ornaments such as rings or headpieces also serve as markers of social identity or status worldwide. Examples include wedding bands, the colorful collars of the Maasai, and diamond necklaces of soci-

ety women (or men). Despite extensive excavation, no beads are known from Europe before ca. 50 kya. Early African sites have yielded a few ostrich eggshell beads in early sites—an unfinished one from South Africa (Boomplaas) dated to ca. 60-80 kya, and several from Tanzania (Mumba) dated directly to between 45 and 52 kya. In 2004, a series of perforated shell beads from the coast of South Africa, dated to 76 kya, made headlines as the oldest evidence for personal ornaments. Even older shell beads have been described from sites in North and East Africa, as well as in sites of early modern humans in the Near East.

The evidence for human burial practices with grave offerings indicative of symbolic behavior within Africa is limited, due in part to the relative dominance of open air excavations where bone preservation is poor, and in part to probable cultural practices of burial away from living sites. Two relatively elaborate cave burials at early dates, however, confirm the antiquity of this practice among modern humans at opposite ends of their early geographic range: an elaborate modern human burial at Qafzeh in Israel dated to 100-130 kya, a time when both modern humans and African faunas expanded into the Levant and the burial of a child at Border Cave in South Africa dated to 66-90 kya. The child burial is associated with what appears to be ocher and has a large perforated *Comus* shell in its chest area. The nearest source for the shell is the Indian Ocean ca. 50 miles or 80 km away. The Qafzeh individual was associated with 71 pieces of red ocher, and also with a perforated bivalve shell. These two sites constitute the earliest clear evidence for symbolic burial with grave goods and red ocher, practices that suggest a belief in the survival of a spirit after death.

Emergence of Humanness: A Gradual Process

The accelerating rate of technological innovation was a stepwise process, not a sudden event related to language. By 70 to 60 kya, well before the out-of-Africa event that led to Neanderthal extinction, anatomically modern humans in Africa, and occasionally in the Levant, had light complex projectile weaponry, fishing and bone fishing spears, long distance exchange networks, ocher, deliberate burial with grave goods, regionally distinctive point styles, symbolic engravings and personal ornaments. Within Africa, there was probably a complex web of inter-regional migration and local extinction that makes the record patchy

and discontinuous. In addition, demographic and climatic factors may affect the degree to which any of these modern human capabilities are expressed. Ethnographic studies suggest, for example, that symbolic expression, subsistence practices, and regional networks intensify under condition of resource stress.

Neanderthals, on the other hand, before 50 kya, had hafted spear points, used a large amount of black coloring materials, and practiced simple burials without offerings or ocher. There is little evidence in this early time range for Neanderthal fishing and none for bone tools, musical instruments, cave art, or personal ornaments. After 40-50 kya, when modern humans were already on the Neanderthals' periphery or perhaps in their midst, Neanderthals developed or adopted some of the same traits—particularly the beads and stone technologies. But they still lacked small light projectile armatures (points) and rarely if ever went fishing. And the really long distance raw materials are only marginally present towards the end of their existence at the northeast edge of their range in Eastern Europe and Central Asia. In both regions we would expect human territories to be very large and populations sparse.

Why was *Homo sapiens* able to replace Neanderthals in Eurasia after 50 kya but not before? There seem to be three possibilities: 1) a sudden genetic mutation, 2) technological superiority, or 3) more sophisticated social networks. These networks, supported by a greater use of symbols or even language, would have buffered humans against risks. A fourth hypothesis is that invading Africans brought with them epidemic diseases to which the Neanderthals had no resistance.

In any event, Neanderthals survived long enough to leave archaeological and/or fossil traces in several sites in southern Europe that are contemporary with sites of early modern humans in Europe over a period of at least 6000-7000 years. Co-existence in the Near East may have occurred over an even longer period. New work on the nuclear DNA genome of Neanderthals even suggests that modern populations in Eurasia (but not in Africa) carry a small percentage (1-4%) of Neanderthal genes, implying that Neanderthals and modern humans interbred in the Near East, before modern humans expanded to the rest of Eurasia. (This and other new genetic studies bearing on human evolution and migration will be covered in a future *AnthroNotes* article).

While the answer to the question of why *Homo sapiens* was able to replace Neanderthals is almost certainly more complicated than any of these three simple hypotheses offered above, and may involve combinations of them and others, the evidence against a revolutionary genetic event is strong when you consider Africa. That continent is characterized by the earlier appearance of technological and economic complexity, as well as of complex symbolic behavior. The patterning of change both during and at the end of the Middle Stone Age period of early *Homo sapiens* is also very different from that consistent with a genetic revolution, as it is both spotty and gradual. Such gradual patterning is much better explained in earlier anatomically modern humans by assuming the existence in earlier anatomically modern humans of modern behavioral capabilities that are variably expressed when conditions call for them. When either climate change or population growth created effective crowding, in an otherwise sparsely inhabited landscape, such pre-adaptation could have become expressed in modern behavioral capabilities.

Conclusion

Currently available data suggest that our ancestors possessed some basic capacities for technological innovation and symbolic behavior before the line leading to Neanderthals in Europe diverged from the line leading to Anatomically Modern Humans (AMH) in Africa, a split which genetics and archaeology concur in dating to between 400 and 800 kya. These more human capacities became more elaborately expressed earlier in Africa because of its larger population, more diversified landscape, and greater potential for interregional interaction. As a result, by 60 kya, AMH entering Eurasia were able to expand and replace Neanderthals, who responded initially with increased expression of some of these capabilities on their own, but were ultimately unable to prevail. In the future, new data from the fossil and archaeological records but also from the evolutionary history of the brain, its faculties, and genes that affect behavior may shed further light on the question of what it means to be human.



Alison Brooks at Olorgesailie, Kenya.

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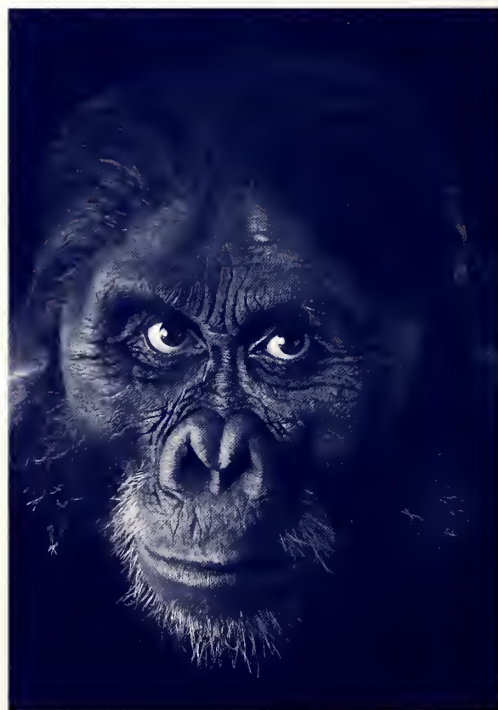
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Australopithecus afarensis. Starting with a cast skull, artist John Gurche builds layers of muscle, fat, and skin to create hyper-realistic busts of human ancestors featured in the new *David H. Koch Hall of Human Origins* at the Smithsonian's National Museum of Natural History.

PRESENTING HUMAN EVOLUTION TO THE PUBLIC: THE SMITHSONIAN'S HALL OF HUMAN ORIGINS

by Rick Potts



At twelve o'clock noon, on March 17, 1910, the Smithsonian's newly built National Museum of Natural History opened its doors to the public for the first time. Exactly one hundred years later the museum chose to celebrate this auspicious occasion with the opening of the long-awaited exhibition, *The David H. Koch Hall of Human Origins*. This major exhibition opened at exactly noon on March 17, 2010 to hundreds of visitors eager to see the widely publicized human origins hall.

The exhibition presents nearly 300 objects, including original fossils and artifacts, along with exact replicas of fragile and unique specimens that must be kept and protected in the countries where they were found. The main purpose of the *Hall of Human Origins* is to show the evidence of humanity's evolution over time; how the development of human features helps us understand who we are as a species today; and why knowing about this process is important. Not just based on Smithsonian research, the exhibit is an international effort built on Smithsonian partnerships with more than 60 research institutions and more than 100 scientists and educators from around the world.

What Does It Mean To Be Human?

The exhibition and its companion website offers the public an opportunity to explore the scientific finds that shed light on one of the significant sparks to human curiosity – our own origins. The primary theme of the exhibition is not an answer, but rather a question: *What Does it Mean to be Human?* This central question goes to the heart of human curiosity: *who* are we as human beings, *how* did we get here, and *where* are we going? By choosing a question for our exhibition theme, the goal is to invite each museum visitor to explore the scientific discoveries about human origins and to connect their lives and personal perspectives to the evidence of how our species evolved.

In the central area of the L-shaped exhibition, visitors are invited to type in their answers to this central question 'What does it mean to be human?' Their responses, which are posted on our web site, www.HumanOrigins.si.edu, help inform us of the immense diversity of thoughts our museum and web visitors have as they encounter the evidence of human evolution. Answers to this question are informed by many perspectives drawn from philosophy, religion, the arts, the sciences, and every-day life experiences.

The Story Unfolds

Fossils and archeological finds highlighted both in the exhibition and website reflect, for example, the roots of walking upright, transitions in technology, enlargement of the brain, changes in the face and the body, and the diversity of species that are part of our evolutionary tree as reflected in our biological ancestors and nearest relatives that



Exhibit hall
photos,
courtesy
Chip Clark
and Human
Origins
Program.

science has so far uncovered. The hall's interactive displays take our visitors back through time to see how these early predecessors lived, the survival challenges they faced, and the elements of humanness they had accumulated at certain points in time.

Every fossil has a story to tell because each one was once part of a living, breathing individual whose species had evolved some combination of the features that define human beings today. As a baseline, each of these species walked upright and had small eye teeth (canine teeth). Bipedality and small canines define all members of our family tree back to at least 6 million years ago. The earliest of these species walked upright and had long, powerful arms—a union of features that persisted for about 4 million years and enabled these oldest ancestors and evolutionary cousins to walk on the ground *and* climb trees to find food and safety.

Later species abandoned their expertise in the trees as they developed stone toolmaking skills and somewhat enlarged brains. Still later species, like *Homo heidelbergensis*, were the first we know of to build hearths and shelters, and to hunt using wooden spears. Later in time, the Neanderthals (*Homo neanderthalensis*) were very clever at making tools and using local food and stone resources; they even buried their dead on occasion and created symbolic artifacts of unknown meaning to us today. However, all of these species, including many side branches, are no longer around; their ways of life now extinct, they leave our own species, *Homo sapiens*, as the last survivor of a once diverse evolutionary tree.

In 1910, the scientific record of human origins consisted of a few dozen fossils, mostly the bones of the famed Neanderthals of Europe. Nearly all of the fossils, archeological remains, and genetic findings that a natural history museum can offer on this subject have been found over the past century. Now, in 2010, the science of human origins is informed by more than 6,000 fossil individuals, ranging from isolated teeth to well-preserved skeletons, spread out over the past 6 million years. These fossils along with hundreds of thousands of archeological remains, which echo the ways of life of early human species, offer a remarkable record of the accumulation of features that make the human species unique.

Milestones in Becoming Human

Humans evolved over millions of years in response to a changing world. The 6 million years of human evolution have comprised one of the most dramatic eras of environmental change in Earth's history, with large swings between warm and cold, and between wet and dry. The *Hall of Human Origins* is the first exhibition on human evolution to explore the drama of climate change and the survival challenges it presented to our early ancestors. These challenges set the stage for the changes – the adaptations – that evolved over time.

The exhibition is organized around a series of displays that present the key milestones in human evolution. In one area, adults and children alike enjoy stepping in an exact reproduction of the oldest known bipedal footprints, 3.6 million years old, made by the species *Australopithecus afarensis*.



(the most famous fossil of which is known as Lucy). Another area shows that, by about 2 million years ago, our ancestors began to delay eating their food, carrying it to places where meat could be butchered and bones with nutritious marrow could be smashed open. Later in time, between 800,000 and 400,000 years ago, there is ample evidence of hearths where food was cooked and of well-made shelters indicating that our ancestors made campsites. Still later, by about 130,000 years ago, early groups of our own species exchanged stone materials across vast distances of more than 100 km. This evidence shows the beginning of social networks that stretched across those ancient landscapes. They didn't have Twitter or Facebook, that's for sure—but they kept track of one another from afar, and they knew who had what to offer!

The exhibition is filled with intriguing highlights along the milestone trail. The fastest pace of brain enlargement began around 800,000 years ago, and led to the evolution by about 200,000 years ago of the two largest-brained species, the Neanderthals and ourselves. By this time, children took a long time to grow up, since large brains take many years to mature. Adults were faced with significant demands to find nutritious food to feed the brain of each child as he or she grew. Challenges, of course, still echo prominently in our lives today and can be traced to the evolution of the big human brain over hundreds of thousands of years and the prolonged growth of the brain in every living person.

The exhibition also explores the oldest stone technologies, which remained largely unchanged for more than a million years. The exhibition shows how the long-lived handaxe tradition eventually gave way to smaller and more innovative technologies: for example, projectile points by 100,000 years ago, used to catch fast and dangerous prey; and sewing needles by about 25,000 years ago, enabling early members of our species to make snug-fitting clothing. Clothing made the difference between life and death as populations moved into ice-age habitats.

Among the most interesting of human capabilities is our use of symbolic language. The oldest clues concerning complex symbols are pieces of pigment—faceted sticks and lumps of ocher (yellowish, redish, brownish in color) and limonite (yellowish-brown color), essentially the world's oldest crayons, dated to 250,000 years old. The use of color to mark objects, or perhaps even the body to create a sense of personal or group identity, is the best evidence we have for when language, the most complex of our symbolic abilities, first emerged.

As visitors explore the Hall and website, there are ample opportunities to learn about our own species, *Homo sapiens*, which evolved around 200,000 years ago. By about 17,000 years ago, all species of early humans except our own had become extinct. Despite our prevalence today, even our species had its endangered moments. Between 90,000 and 70,000 years ago, as African environments oscillated between drought and moist times, the population that gave rise to almost all of the genetic diversity among the world's



peoples today had dwindled dramatically to somewhere between 10,000 and 600 reproducing adults. We almost became extinct. However, by that time, *Homo sapiens* had developed a certain resilience in the face of millions of years of survival challenges.

By about 12,000 years ago, pockets of people in several regions began domesticating some plants and animals. These activities ultimately gave rise to the agriculture on which modern societies depend. The exhibition provides an opportunity to contemplate the enormous pace of population growth since that time, our deep influence on the planet, and how our species became a turning point in the history of life. Among the Hall's many interactive displays, one of the most intriguing is a game called 'Keep Your Species Alive,' in which the players imagine the significance of key decisions for the future.

Reflections

As the curator of the *Hall of Human Origins*, I began to develop an environmental approach to the exhibition soon after arriving at the Smithsonian in 1985. Twenty-five years ago, it was a difficult decision to leave Yale University, where

I was a young assistant professor, working in a setting with great potential for developing my research career. Eventually, I saw the move to the U.S. National Museum as a special opportunity not only to lead digs and expeditions but also to make sure that the profound questions of human origins and the scientific finds that illuminate these questions would not be confined to a university classroom. My transition to the Smithsonian meant an opportunity to bring research discoveries on human evolution to the widest public audience.

It did not happen all at once, though. In fact, it took nearly 20 years to assemble the best combination of people. John Gurche, to name just one early member of our team, is the foremost artist-anatomist in the lifelike reconstruction of early human species. John is responsible for the astonishing reconstructions of the heads and statues of several early human species that are featured in the Hall.

The 20 years also gave me time to explore new scientific avenues, which ultimately shaped the exhibition. After several years of digging in the Great Rift Valley of southern Kenya, at the stone handaxe site of Olorgesailie, I realized that what I thought we knew about the ancient setting of human evolution—long assumed to have been the African savanna grassland—was by no means a single, consistent environment. The geological clues indicated, instead, that the climate kept changing.

As I delved into the environmental sciences, the more I realized that rather than any one environment or trend, the continual shifting of the landscapes where early humans lived characterized the period of human evolution. This was a story worth telling—and a huge area of scientific investigation that had not yet been presented in a public exhibition.

By 2005, it became one of the museum's top priorities to present this environmental theme along with the vast number of fossils found over the previous two decades. By January 2007, our exhibition core team began to meet, and a three-year period for developing the entire Hall was placed on a fast track to develop all its interactive displays, the many objects for people to see, and the state-of-the-art reconstructions of our early ancestors.



Back to the Beginning

On the evening of March 17, the Smithsonian hosted a gala dinner to commemorate the opening of the *Hall of Human Origins* and our museum's Centennial. The dinner honored Mr. David Koch and Dr. Peter Buck, the exhibition's two principal benefactors. Meave and Richard Leakey among other notable scientists attended, as did members of Congress, the Smithsonian leadership, key members of our exhibition team, and many other fascinating people.

I had dreamed of this exhibit off and on for 25 years and then almost miraculously I had the opportunity to work on it nearly every day with incredibly talented exhibit designers, writers, tech experts, educators, and fellow scientists. I had not thought much about the final day actually arriving. Still, as the long-awaited day unfolded, I could not help think that it was passing way too quickly!

In many conversations that evening, I kept mentioning the exhibition tours we were to give in the coming days, the lecture series that would start in a couple of weeks, and the network of educators and scientists eager to help bring the exhibition's ideas and messages to the American and international public. Gradually, it dawned on me that the opening of the Hall was not the end of the road, but the start of an ongoing endeavor of great responsibility.

I am eager to return to the field and continue our digs in Kenya, China, and other countries. But now there is more to it than that. Our Smithsonian team can hardly wait for new discoveries by researchers all over the world that will make the updates to our exhibition, additions to our new website, and our educational events for the public exciting possibilities for the future. As with science itself, where each new significant discovery leads to new ideas and explorations, I now see that our efforts to present the science of human origins to the public will lead to new ways of making the science as exciting and as relevant to as many people as possible.

The opening of the exhibition has become in retrospect the signal of a terrific beginning. If there is any answer the exhibition gives to the question 'What does it mean to be human?' it is that 'being human' has been, in part, a matter



Rick Potts in his Smithsonian office.

of 'becoming human'—a wondrous process of change over time, an ancestry that connects all people to one another and our species to every form of life on planet Earth. Every day this hall and its rich website will continue to help people explore and learn about this amazing scientific quest.

For further information about the exhibit and the Smithsonian's Human Origins Program, consult its companion publication and website:

Potts, Richard and Christopher Sloan. 2010. *What Does It Mean to be Human?* National Geographic.

Human Origins Website: <http://humanorigins.si.edu/>

Rick Potts is Director, Human Origins Program, and Curator, "The David H. Koch Hall of Human Origins."

TEACHERS CORNER: RESOURCES FROM THE SI HUMAN ORIGINS PROGRAM

by Briana Pobiner



In the previous article, Curator Rick Potts discussed the new *David H. Koch Hall of Human Origins*. He noted that, not unlike scientific inquiry itself, the exhibition's theme is a question rather than an answer: *What does it mean to be human?* This theme is even more prevalent on the new web site, www.HumanOrigins.si.edu. On this site, we have the opportunity to share the wealth of evidence for, and current research about, human evolution with millions of people from around the world. While the website was created with diverse audiences in mind, one of the primary audiences is teachers. This Teachers Corner summarizes the resources currently on the human origins website of interest to teachers and other educators. The website is designed to be easily expandable as we continue to add new content and features. We welcome feedback on the website; please email your suggestions and comments to HumanOrigins@si.edu

HUMAN ORIGINS WEBSITE:

Education

A variety of teacher and educator-specific resources are assembled in the Education section of the web site: <http://humanorigins.si.edu/education>. These include:

- 1) A downloadable, PDF "Educators Guide" to the exhibition hall, specifically designed for class field trips. In lieu of offering tours for school groups, the Educators Guide is designed with pre-, during, and post-visit activities for students in grades 5-12. There are data collection sheets for students to fill out during a visit and hot links within the

PDF connecting to other areas of the website. These sections correct common misconceptions about human evolution and offer further readings (books and websites).

- 2) Links to lesson plans on human evolution for use in the classroom. Borrowed from the "Understanding Evolution" website (University of California Museum of Paleontology), all these plans have been tested and vetted by teachers.
- 3) A private discussion forum for educators, where teachers can discuss ways to best use the website in the classroom, exchange ideas about teaching human evolution, etc.
- 4) Information about the HopEdNet (Human Origins Program Education Network), a nascent large-scale, long-term effort to bring educators and scientists together to focus on teaching and learning about human origins.
- 5) A section for college-age students with links to summer field schools.
- 6) Fun Facts— short tidbits about human evolution that are great ways to get students thinking about the topic.

Resources

The resources section of the web site <http://humanorigins.si.edu/resources> also has a variety of useful areas:

- 1) A general introduction to human evolution.
- 2) A human evolution glossary. Definitions of terms also are available by hovering a mouse over those terms anywhere on the website.
- 3) A section on "What's Hot in Human Origins?" keeps visitors up-to-date with the latest key discoveries in this dynamic field of research.

- 4) Links to all the site's multimedia resources—podcasts (audio), videos, and photograph slideshows.
- 5) A “How Do We Know?” section, which uses material from the exhibition to outline some examples of how we know what we know in the science of human origins (a great example of scientific knowledge in general).

FAQ (Frequently Asked Questions)

Hidden in the top right corner of the website is a FAQ section <http://humanorigins.si.edu/faq>, which features a growing list of Frequently Asked Questions about human evolution—and their answers. Some examples include “How do scientists know the age of fossils?” “How does evolution explain complex organisms like humans?” “How are humans and monkeys related?” and “Can the concept of evolution co-exist with religious faith?” In addition to this list over time, we will be drawing from the Evolution FAQ kiosk in the Hall of Human Origins, where visitors can type in their questions about human evolution.

Human Evolution Evidence

While many of this section's resources will likely be useful, including a lightbox feature for large format photographs of fossils and artifacts, three particular sections can be highlighted:

- 1) Human Evolution Evidence is one of the most unique and popular features of the website with a 3D Collection <http://humanorigins.si.edu/evidence/3d-collection>. This collection features rotatable, 3-dimensional scans of hundreds of fossils and artifacts, most of which are found in the *Hall of Human Origins*. One of the most useful features of this teaching collection is that each object is available in a 3D PowerPoint slide. These rotatable objects can be used as part of your own presentation!



- 2) Building on this 3D collection is our Mystery Skull Interactive <http://humanorigins.si.edu/evidence/human-fossils/mystery-skull-interactive>, where students become scientists! A mystery skull is presented. Comparison to other known skulls can help determine what species it belongs to—in 3D. Hints for each mystery skull are available to help students learn how to look at skulls and make comparisons among them.

(continued on next page)

3) Also in this area of the website are detailed summaries of each early human species. (Please note that the term “early human” is used instead of “hominin,” following on the terminology used in the exhibition.) <http://humanorigins.si.edu/evidence/human-fossils/species> includes an audio pronunciation guide, a reconstruction of what the species may have looked like, information about when and where fossils of that species have been found (and when it was first discovered), estimated height and weight, and information about the species’ unique adaptations. Short bibliographies are available for students writing reports or papers.

Human Evolution Research

This section goes into more detail about the research that the Human Origins Program team is undertaking. Over time this section will feature research by some of our research associates and other interesting projects. Similar to the Human Evolution Evidence section, some pages feature more concise information, while others have more detail, including bibliographies. There are also three interactives in this section:

- 1) **Ologesailie: Adventures in the Rift Valley** <http://humanorigins.si.edu/research/east-african-research/adventures-rift-valley-interactive>. In this interactive, students again get to be the scientists – this time, on a field expedition to Ologesailie, the Smithsonian’s research site in southern Kenya. Students search for evidence across the landscape at Ologesailie to answer a variety of research questions, keeping a notebook to track their findings along the way.
- 2) **Fossil Forensics** <http://humanorigins.si.edu/research/fossil-forensics-interactive>, where students can see how scientists ‘read’ bones for forensic-style clues.
- 3) **Timeline Interactive** <http://humanorigins.si.edu/research/climate-research/timeline-interactive>, which features clickable links to early human species, fossils specimens, human evolution milestones, and climate change evidence, all in the context of a timeline with a zoom feature so students can explore particular times in human evolution that they find most interesting.

Broader Social Impacts Committee

On the Home Page is a section called “Human Evolution: Religious Perspectives,” which links to the pages about the Broader Social Impacts Committee <http://humanorigins.si.edu/about/bsic>. Recognizing the challenges posed by evolution, and especially the topic of human evolution for some people, the Human Origins Program has assembled this committee, comprised of people from diverse religious and philosophical communities from around the United States. The committee is assisting in public communication and dialogue surrounding the exhibition *What Does It Mean To Be Human?* and helping promote outreach efforts in human origins. The committee also is continuing to develop web-based resources, which teachers may find useful in the classroom.

SOCIAL MEDIA:

Become a fan of the Smithsonian’s Human Origins Program on Facebook <http://www.facebook.com/smithsonian.humanorigins> and follow us on Twitter <http://twitter.com/HumanOrigins> to keep up with even more of the latest discoveries in, and conversations about, human origins research.

Briana Pobiner is Education & Outreach Specialist, Human Origins Program.

[See the article, “Teaching Human Evolution: Websites,” by B. Pobiner in the Fall 2008 issue of *AnthroNotes*, p. 14.]

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NEW PERSPECTIVES ON THE EVOLUTION OF BIPEDALISM

by Alison S. Brooks



Early scholars of natural history recognized that bipedalism, tool use, and language were among the most important defining characteristics of our species. In 1780, Blumenbach actually classified humans in a separate order, the “Bimana” or two-handed animals, implying only two limbs used for locomotion. Even as late as the 1950s, many thought that large brains and bipedalism had evolved together, an impression supported by the large brain of the “Piltdown Man” forgery. But as recent fossil evidence makes clear, bipedalism actually developed long before there was any sign of enlarged brains, tool-making, or any kind of symbolic behavior that would suggest language abilities.

Why did our lineage adopt such an unusual way of getting around, a way that is exceedingly rare among mammals? There are other bipeds, but kangaroos move by hopping on their hind legs, balanced by a long heavy tail, and many birds such as ostriches run on the ground with bent knees, also balanced by a tail. Humans are the only striding, tailless bipeds. Because we started out as tailless apes, our bodies had to change in many ways to balance the body over that one leg during walking and running. Our head is balanced atop the spine rather than out in front of it, and our spine itself is S-curved, to balance the mass of the upper body over the legs. This alone causes us a great deal of grief by putting strain on the lower back and neck. Our pelvis changed from a long linear shape with flat blades (ilia) extending up the back to a basin shape that cradled the abdominal organs but created problems later on in evolution for birthing a large-brained baby. The new shape of the pelvis changed the position of the muscles attached to those blades, which were used to pull the leg back but now extend to the side over the hip joint to keep you from falling over when you pick up one leg and stand on the other. Otherwise (or if those muscles aren't functioning well) you would have to walk the way chimpanzees and some other four-footed animals do—leaning sideways over the leg you stand on to keep your balance and

prevent falling towards the leg you are lifting. The hip joints are bigger than in apes of comparable body weight since they carry our full weight whenever we are moving or standing. To make it easier to balance on one leg, our knees are positioned directly under the body, which makes the thigh bone (femur) slant inwards from hip to knee. Finally our foot changed from a grasping appendage to a propulsive one, with a bigger, straighter and stronger big toe in line with the shorter lateral toes for pushing off, and with both a longitudinal and transverse arch to stiffen the foot for toe-off. This literally puts a spring in our steps when we run.

Fossil Evidence for Bipedalism

Even the very fragmentary fossil remains from early in human evolution suggest that adaptation for bipedalism was an early and essential step, so to speak, on the road to becoming human. At 6-7 million years ago (mya), two early ancestors represented by the fossils *Sabelanthropus tchadensis* from Chad and *Orrorin tugenensis* from Kenya appear to have already changed their way of getting around. The hole in the base of *Sabelanthropus*'s skull for its spinal cord had become reoriented so it points downward rather than backward, and it is positioned a little further forward suggesting that the head was becoming more balanced on top of a vertical upper spine. The cross-section and width of the femur of *Orrorin* suggests that it was already bearing more weight, although the hip joint would have been smaller than in modern humans. In addition, the long narrow neck of the femur, which joins it to the hip socket, indicates that the pelvis (which is missing) was already much broader than in apes. The curved toe and finger bones and the muscle markings and shape of the upper arm bone suggest that *Orrorin* also spent a lot of time climbing around in trees, to sleep, eat, or escape from predators.

An almost complete skeleton of *Ardipithecus ramidus* from Ethiopia, dating to 4.4 mya and published in October 2009, has an even more curious combination of traits. The upper blades of the pelvis (ilia) are shorter and broader than in apes, and the pelvis as a whole apparently has a basin shape, suggesting a degree of adaptation for upright walking. But the foot retains a fully opposable big toe for grasping and climbing in trees, and it does not have either a longitudinal or a transverse arch.

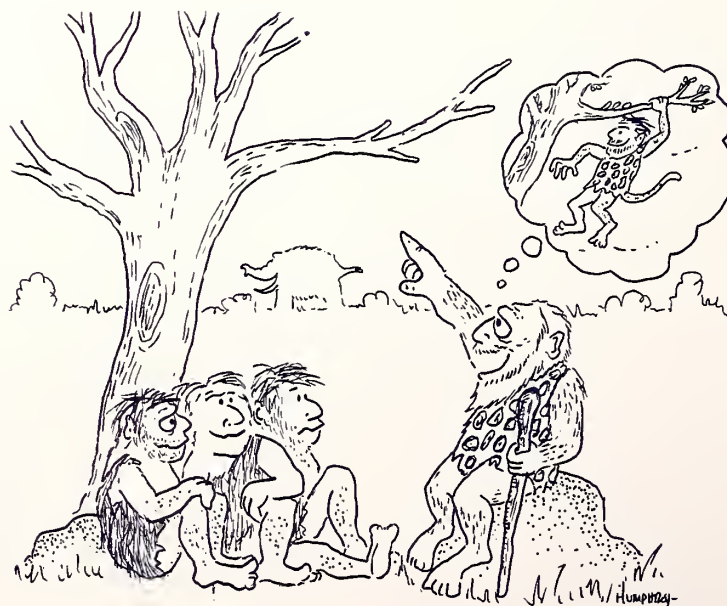
From 4.4 to ca. 1.9 mya, members of the genus *Australopithecus*, whose most complete skeletons so far are Lucy and the recently reported skeletons of *Australopithecus sediba* (*Science* 4/9/2010), were more committed to habitual bipedal walking, with an S-curved spine, a very wide basin-shaped pelvis, an inward-slanting femur, a large big toe close to the other shorter toes, an expanded heel, and some degree of arch in the foot. That *Australopithecus* walked upright is also demonstrated by the footprint trail at Laetoli, (near Olduvai Gorge in northern Tanzania), where a larger and a smaller *Australopithecus* walked together through wet muddy ash 3.6 mya. Their stride may have been different from ours, however, as their toes were still long and curved for climbing in the trees, and their legs were short compared to their arms.

Only with *Homo erectus* at ca. 1.8 mya do we see a full-commitment to life on the ground and reduction or elimination of many of the features that made it easier to get around in the trees: longer arms, an upwardly oriented shoulder joint for hanging, and grasping toes with a limited arch. The “Turkana boy” skeleton of an adolescent dated to 1.5 mya has the long legs and basin-shaped pelvis of a fully bipedal human, while a slightly earlier foot skeleton from Olduvai Gorge has short toes and a human-like arch. A recently published set of footprint tracks in Kenya from 1.5 mya suggests real “toe-off” striding and a fully-

human arch. Variations in the pelvis after *Homo erectus* apparently have more to do with providing space for a larger-brained infant than with perfection of bipedal locomotion.

Why Walk on Two Legs?

Why did our lineage adopt this peculiar mode of getting around? It would not have made it any easier to escape from predators—most chimpanzees and all monkeys can outrun us over short distances. An early argument held that bipedalism developed to free the hands to make tools. But as there is no sign of elaborate tool-making for a least the first 3-4 million years after the first bipedal members of our lineage such as *Sabelanthropus* and *Orrorin*, it seems more likely that later tool-makers took advantage of hands that were already partly freed. Another argument suggests that bipedalism developed to facilitate moving between widely-spaced feeding trees, but *Ardipithecus* seems to have inhabited fairly dense woodland. Did we become bipedal to see over the tall grass? (My own experience in the western Rift Valley suggests that the grass in many places is more than six feet high, and Lucy was about 3.5 feet tall.) Two other theories that are plausible but difficult to demonstrate are 1) that bipedalism makes a primate appear larger and more threatening to potential challengers and predators (male gorillas run short distances on their hind legs to threaten intruders) or 2) that bipedalism makes it easier to carry



food and infants to a safe place to feed (but see the comment on Ardi's likely closed woodland habitat, above). And even if we initially became capable of bipedal walking for one of the above reasons, why abandon the safety of the trees altogether after 1.8 million years ago, since by then our ancestors had lost their climbing toes, short legs, long arms and upwardly mobile shoulders for hanging from branches?

Born to Run?

A new theory, proposed by Bramble, Lieberman and colleagues in a series of papers from 2004 on, is that it is not about bipedal walking at all. Rather we were "born to run," and it is running that constitutes one of several major adaptations that helped shape our bipedal morphology after *Australopithecus*. How can this be, as human runners are relatively slow. Human legs and feet are well-adapted, however to endurance running. In jogging or "marathon-mode," the long spring-like tendons in our legs (such as the Achilles tendon) and the arches in our feet store and then release energy like a spring during one part of the running step for later release. Our shorter toes are well-adapted for pushing off, while long legs make it possible to cover a given distance in fewer steps. Finally our long waist and other structures allowed the upper body to counteract the twisting forces generated by running and stabilize the body. This is why runners feel compelled to pump their arms back and forth in opposite directions to the corresponding legs when they run. Also, a new (in *H. erectus*) ligament to the back of the head stabilizes the head on the spine. Running also makes maximum use of our large gluteal muscles, which first become enlarged in the genus *Homo*, while walking uses them only minimally.

In addition to these adaptations in our lower limbs, specializations for heat loss allow us to run for exceptionally long distances even in the middle of the day. These adaptations include our elongated bodies compared to apes, hair loss, increased number of sweat glands, mouth-breathing while running, and possibly adaptations of the circulatory system to better cool the brain.

Bramble and Lieberman compare our endurance running to trotting, which several running mammals are able to maintain for considerable periods of time. Well-conditioned humans, however, "trot" faster than dogs and

can even out trot horses in hot conditions. Mammals can move faster when galloping than trotting, but they cannot pant and gallop at the same time. Since non-human mammals cool mostly by panting, they can die of heat exhaustion (hyperthermia) when forced to gallop for extended periods of time in the heat. The authors argue that our human ability to run with long strides, sweating, and other heat-loss adaptations account for why so many humans, even into their 70's and 80's, are able to run marathons.

An ability to run long distances in the heat of the day would have conferred considerable advantages on early humans, who incorporated increasing amounts of meat into their diets but seem to have lacked sophisticated weaponry for hunting or for challenging other carnivores at kill sites. In 2006, Liebenberg published a study of so-called persistence hunting by modern San peoples in the Kalahari Desert in Botswana. (One of these hunts can be viewed at (http://www.youtube.com/watch?v=fUpo_mA5RP8.) Hunts in the heat of the day last from two to eight hours of running after the animal through sand and brush over distances of 25-35 km. at average speeds of 6-10 km/hour, which is not especially fast even by marathon standards. At this point, the animal collapses from heat exhaustion, sometimes not even requiring the hunter to finish it off.

Since persistence hunting requires considerable tracking abilities, has a risk of dehydration, and is rare among modern hunters, Pickering and Bunn challenged Bramble and Lieberman's scenarios. Did early humans who lived in savanna woodlands rather than in desert bushlands have the ability to track animals as the San do? Lieberman and others replied that even non-human carnivores have the ability to follow prey, that following a wounded animal also would have required tracking skills, and that persistence hunting even today is often more successful than hunting with a bow and arrow. Further, hunters can carry water in an ostrich eggshell or a skin bag. Did they actually run down animals? We can only ask how they might have acquired large prey otherwise, without sophisticated weaponry. Running may have developed out of an earlier adaptation to bipedal walking as a way to cope with increasing aridity and use of open environments by our ancestors after 1.8 mya.

Further work on running, much of it by Lieberman, his colleagues and students, has demonstrated that shorter toes lower the energetic cost of running but not of walking, and that habitual barefoot runners (studied in America and Kenya) land on the balls of their feet (or sometimes on the mid-foot) rather than on the heel. Even with a highly cushioned modern running shoe, landing on the heel generates more “shock” or force that travels up the leg, while landing on the forefoot almost entirely eliminates any collisional force on impact, making barefoot running comfortable and easy to do on even the hardest surfaces. Studies on the developmental history of these adaptations in childhood and on physiological effects of hormones on bone growth have also added to our understanding of this fundamental and unique human adaptation.

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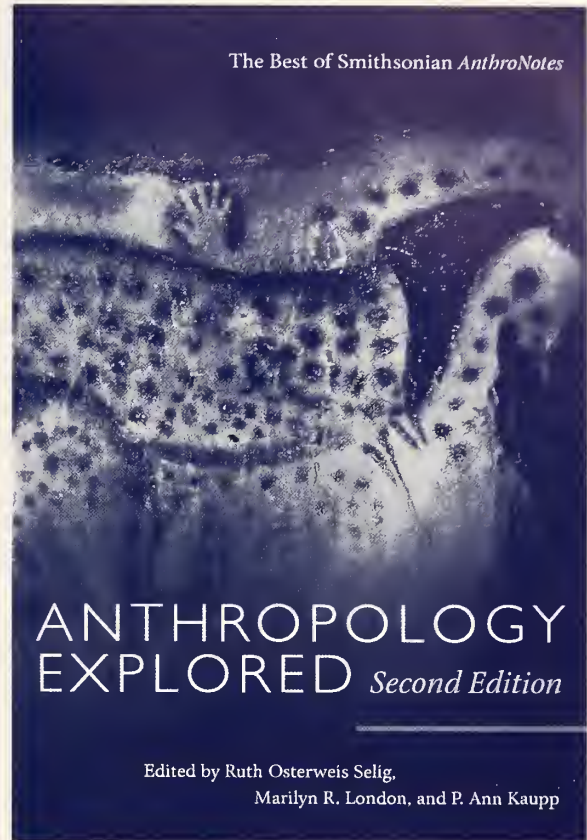
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